CHILLING AND TRANSLOCATION INHIBITION[1, 2, 3]

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ABSTRACT

The effect of chilling on translocation in higher plants was reviewed by separate consideration of path, sink, and source-cooling effects. The response of the sink to chilling indicates that the effect is mainly due to the inhibition of a metabolic process, while the response of the path to chilling suggests that the effect is mainly due to physical damage such as alteration of membranes. Sugar beet *Beta vulgaris* L. shows a rapid recovery of translocation during chilling, and bean *Phaseolus vulgaris* L. shows a very slow recovery; northern and southern ecotypes of Canada thistle, *Cirsium arvense* L., resemble beet and bean, respectively. Differing bases for chilling-inhibition mechanisms in the subdivisions of the translocation system are suggested by the analysis of kinetics of inhibition and recovery during localized chilling of these parts.

INTRODUCTION

The rate and pattern of distribution of phloem-limited translocation is closely attuned to supply and utilization within a plant. It is not surprising that chilling affects translocation of sugar, sometimes profoundly inhibiting the process. It has been noted that inhibition of translocation parallels inhibition of other metabolically dependent processes, such as cyclosis (Webb and Gorham, 1965; Webb, 1967). The mechanism responsible for reduction of translocation in a chilled plant has not been established, although chilling inhibition of translocation has been the subject of numerous studies, including those of Hull (1952); Kursanov (1963); Esau, Currier, and Cheadle (1957); Whittle (1964); Webb (1967); Swanson and Geiger (1967); Webb and Gorham (1965); Hewitt and Curtis (1948); and Ford and Peel (1967).

LOCALIZED COOLING

A striking feature observed in chilling studies is the effectiveness of a few centimeters of cooled stem or petiole in decreasing translocation. When an entire plant is so treated, the translocation rate responds to temperature in a manner characteristic of an energy-dependent, physiological process. This temperature-response pattern, observed in bean, tomato, milkweed (Hewitt and Curtis, 1948), *Pteridium* (Whittle, 1964), and soybean (Thrower, 1965), shows an optimum range of 25 to 30°C and a marked degree of inhibition below 5°C. If the temperature treatment is restricted to a few-centimeter-long zone of a stem or petiole, a response curve similar to the one observed for systemic cooling is obtained. Inhibition of translocation by localized cooling of the path has been reported for bean (Bohning, Swanson, and Linck, 1952; Curtis and Herty, 1936; Kendall, 1952; Swanson, 1959; Swanson and Bohning, 1951; Swanson and Whitney, 1953), tomato (Bohning, Kendall, and Linck, 1953), squash (Webb and Gorham, 1965; Webb, 1967), and soybean (Thrower, 1965). Notable variations in the response are cited by Hull (1952), Swanson and Geiger (1967), and Ford and Peel (1967).

The term *path* is used in this study to designate the larger veins of the leaf and the vascular bundles in the petiole and stem. The phloem of these structures is primarily involved in conveyance of assimilate, rather than in its uptake or unloading. This distinction has a basis in the structure and relative size of the sieve tubes and companion cells (Geiger and Cataldo, 1969).

The similarity between the response to systemic cooling and the response to

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localized path cooling in a number of different plants is consistent with the view that the key metabolic processes motivating translocation are located in the translocation path. The possibility still remains that path chilling exerts an overriding control over the translocation process in some plants, without directly inhibiting the key process driving solute movement. Evidence for separate mechanisms of inhibition in various parts of the plant is examined in the following sections.

POSSIBLE MECHANISMS OF INHIBITION

Several workers, including Esau, Currier, and Cheadle (1957), Bohning, Swanson and Linck (1953), Thrower (1965), and Peel and Ford (1967), have pointed out that low-temperature inhibition of translocation could be the result of a physical effect, for example, increased viscosity of protoplasm or of sieve-tube cell sap, or the result of a direct effect on respiratory reactions supplying the energy for the translocation process. The existence of more than one mechanism for low-temperature inhibition in the various portions of the translocation system has not been studied in detail to date.

An observation pointing up this possibility is the difference in degree of inhibition resulting from systemic chilling versus chilling restricted to a zone of stem or petiole. Crafts (1932) has observed a greater inhibition of exudation from cucumber stem when the entire plant was kept at 17°C than when the stem was locally chilled to 1 to 4°C. Swanson (1959) drew attention to the greater degree of inhibition of translocation in bean at 10°C when the entire plant was treated, than when only a portion of the path was chilled. These studies do not indicate whether the increased inhibition from systemic cooling is due to the greater extent of the treated region or to cumulative effects on separate temperature-sensitive mechanisms in the two types of experiments.

RECOVERY FROM CHILLING

Gradual recovery from inhibition when path cooling is prolonged also suggests that there may be a mechanism for low-temperature inhibition of translocation, in addition to direct inhibition of the key process which moves the translocate. Use of different durations in translocation experiments led to the discovery of a decrease in the effectiveness of a given low temperature with time. Curtis (1929) found that keeping the petiole of kidney-bean leaves at 1 to 4°C greatly inhibits translocation, as measured by leaf-weight loss over a 17- to 20-hour period. At 7 to 12°C, the loss is not significantly lower than that observed in the controls held at 17 to 24°C. Using a six-hour measuring period, Curtis and Herty (1936) later showed that translocation at 7 to 12°C is reduced significantly over that at 24°C. A comparison of these data indicate that, with time, at least partial recovery from inhibition occurs at 7 to 12°C. Acclimation was also noted by Swanson and Bohning (1951) in experiments with bean in which translocation was measured after 65 to 135 hours at 10°C.

One explanation for this recovery is a homeostatic adjustment of the energy-releasing process to low temperatures. Recovery over a short time, as reported by Swanson and Geiger (1967) and by D. E. Bayer (personal communication) (figs. 2, 3, 6–8), which is less likely to be due to this type of adjustment, can be interpreted to mean that inhibition by path chilling is due to a mechanism, such as increased viscosity or path impedance, which does not directly interfere with the process which moves the translocate. The latter explanation is compatible with those translocation theories which propose that the process driving translocation is located in the source or sink, and which envision a relatively passive role for the path (Bauer, 1953; Esau, Currier, and Cheadle, 1957; Muller and Leopold, 1966).

SEPARATE MECHANISMS

The possible existence of separate temperature effects proper to the various

translocation-system subdivisions suggests the desirability of studies addressed to the following questions.

1. What portions of a translocation system are susceptible to low-temperature inhibition?
2. Does the time-course of low-temperature inhibition and recovery differ significantly in the source, sink, or path subdivisions of the translocation system?
3. What mechanisms are responsible for producing low-temperature inhibition of translocation during localized chilling of the various subdivisions of the translocation system?

In a review of environmental effects on organic translocation, Nelson (1963) recommended consideration of the effect of environmental stress on translocation in terms of the effect on its several sequential processes. Cooling, for example, would affect each of these processes to a certain extent and by a different mechanism, ultimately giving rise to the observed temperature effect. Localized cooling of each individual portion of the translocation system enables us to investigate the role of low temperature in the various component subprocesses of translocation, and so contributes to an understanding of those mechanisms responsible for low-temperature inhibition.

The experimental system employed in the experiments reviewed in this paper permits a continuous record of mass-transfer rate from a source leaf under various experimental conditions (Geiger, 1966; Geiger and Swanson, 1965; Swanson and Geiger, 1967). The method provides a means of observing both long- and short-term adjustments when experimental conditions are changed.

PATH CHILLING

Previous studies by Child and Bellamy (1919), Curtis and Herty (1936), and Swanson and Geiger (1967) indicated that there is some recovery of translocation through a chilled section of petiole as the treatment is continued. The use of steady-state labeling has made possible continuous monitoring of the translocation rate following onset of inhibition and of recovery during low-temperature treatment. Experiments with *Phaseolus vulgaris* undertaken by Geiger and Cataldo (in preparation), in which a 2-cm length of petiole was cooled to 3°C, reveal rapid, complete inhibition of translocation, with no sign of recovery over several hours (fig. 1). Translocation from the source leaf resumed 45 minutes after warming

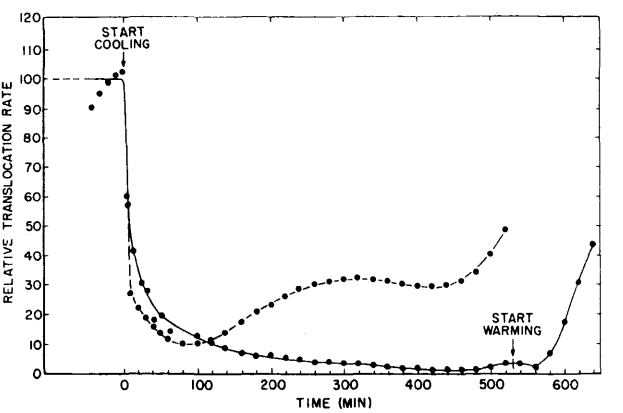

FIGURE 1. Comparison of translocation rates through a 2-cm zone of bean petiole at 3°C and at 7°C. Upper curve 7°C treatment; lower curve 3°C treatment. Both petioles at 25 to 28°C except during treatment period. (Geiger and Cataldo, in preparation)

of the petiole to room temperature and, by three hours, it attained a rate 60–65% of the pre-cooling level. The delay was similar to the recovery lag noted by Webb and Gorham (1965), when the primary leaf node of squash plants was cooled to 0°C and subsequently returned to 25°C, and to the 5- to 20-minute lag reported by Thrower (1965) when the petiole of soybean was chilled.

When the temperature of a 2-cm length of bean petiole was lowered to 7°C, instead of 3°C (Geiger and Cataldo, in preparation), translocation was inhibited to about 10% of the pre-cooling rate, and recovery began after several hours (fig. 1). After four hours of cooling, translocation had increased to 30%, and after nine hours it had reached 50% of the pre-treatment rate. Both the data shown in figure 1 and results from similar experiments show that the degree of inhibition and the time required for recovery of translocation during localized cooling of a petiole zone in bean depends on the temperature used.

A kinetic study of the effect of cooling a 2-cm portion of sugar-beet petiole to near 0°C, reported by Swanson and Geiger (1967), revealed a significantly different response from that of bean. In the sugar beet there was a rapid onset of nearly complete inhibition, as with bean, but within one to two hours complete recovery to the original translocation rate had occurred (fig. 2). When the petiole was

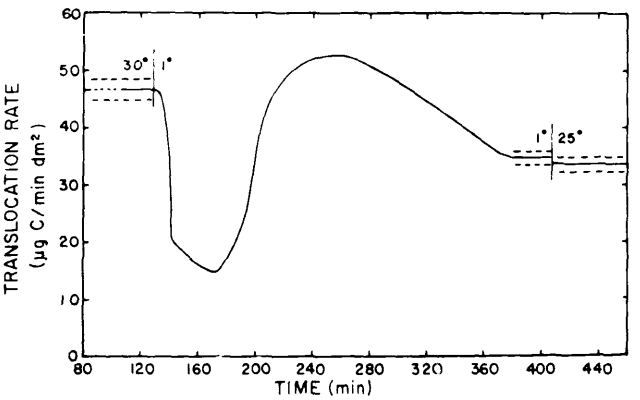

FIGURE 2. Time course of translocation through a 2-cm zone of sugar-beet petiole at 1°C. Petiole zone temperature indicated above the curve. (Swanson and Geiger, 1967)

subsequently cooled, a similar cycle of inhibition and recovery again occurred. Warming the petiole after recovery had occurred produced little or no increase in translocation rate. A translocation rate of approximately 40 µg carbon minute^{-1} dm^{-2} from the source leaf, within the normal range for plants not subjected to cooling, was maintained, even after 25 hours of petiole chilling; only a transient increase in rate occurred when the petiole zone was warmed to room temperature (fig. 3). Apparently the recovery noted in bean plants, after many hours or days of petiole cooling, occurs within one or two hours in sugar beet plants. Part of the data of Hull (1952), which is often quoted as indicating a Q_{10} of one or less for translocation, was gathered from sugar beet plants with a petiole zone held at 1 to 3°C for six hours prior to labeling with ^{14}C-sucrose. Presumably the observed lack of temperature dependence was the result of recovery from temperature inhibition prior to labeling. In a comparison of response in younger and older shoots, Ford and Peel (1967) observed that path chilling causes a decline in translocation rate in 3- to 5-week-old willow shoots, while it causes an increase in translocation rate in 2- to 3-year-old stems of the same plant.

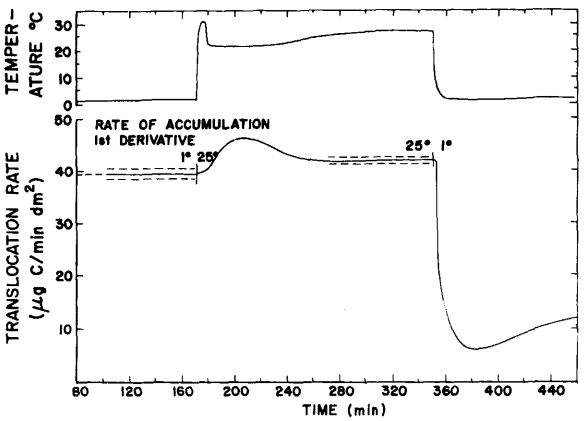

FIGURE 3. Time course of translocation through a 2-cm zone of sugar-beet petiole held at 1°C for 25 hours. Temperature treatment of petiole zone shown above the curve. Total duration of first cooling period 25 hours. (Swanson and Geiger, 1967)

SINK CHILLING

Complete recovery from petiole chilling, such as is found in sugar beet, permits a study of the time course of low-temperature inhibition caused by localized chilling of the sink region, without the overriding influence of inhibition in the translocation path. Linck and Swanson (1960) noted inhibition of translocation into a developing pea pod when it was cooled to 7°C, but the question of how much of the observed effect was distinct from the path-cooling effect remains unresolved. In plants such as sugar beet, continued movement of sucrose through the chilled translocation path, after an initial short recovery period, makes it possible to observe separate low-temperature inhibition as a result of sink cooling.

A sink-chilling study was carried out in sugar beet by cooling beet, crown, and sink leaf to 0°C (Geiger, 1966). A pattern of inhibition consisting of four phases was observed (fig. 4). The temporary decline, followed by recovery, resembles the results of petiole cooling and may be due to the same mechanism, because a considerable length of translocation path is being cooled. Following recovery, translocation again declines and eventually reaches a plateau at 35 to 45% of the precooling rate. Even when cooling is continued for 24 hours, the rate of translocation remains inhibited to approximately 35% of the rate observed at room

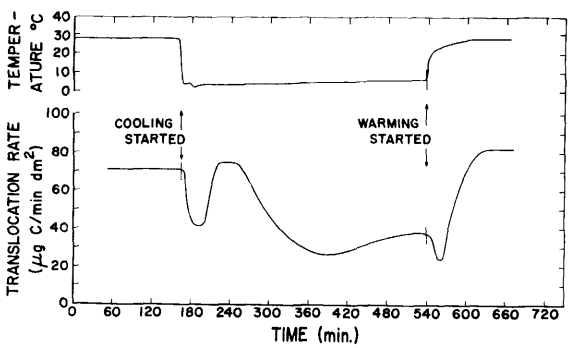

FIGURE 4. Time course of translocation into a chilled-sink region in sugar beet. Treated-sink region includes roots, beet, crown, and sink leaf. (Geiger, 1966)

temperature (fig. 5). In sugar beet, the time course of inhibition during sink cooling clearly differs from the pattern observed during path cooling.

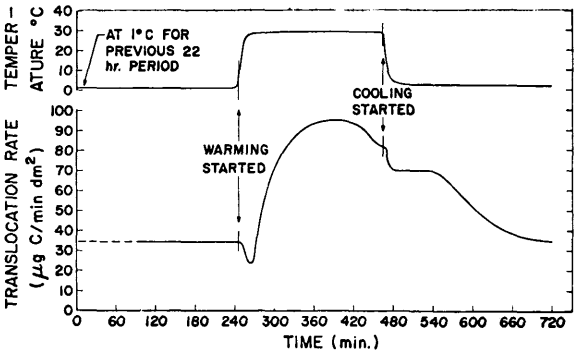

FIGURE 5. Time course of translocation into a sugar-beet-sink region following long-term chilling. (Geiger, 1966)

MECHANISM OF LOW-TEMPERATURE INHIBITION

Rapid recovery from localized path-chilling inhibition of translocation as found in sugar beet, when contrasted with the long-range persistence of sink-cooling inhibition, suggests that there are at least two distinct mechanisms by which low temperature affects translocation in these two portions of the translocation system. Possible mechanisms for low-temperature inhibition of translocation include physical effects, such as chilling-induced changes in structure of colloids, membranes, or organelles, which would alter permeability or resistance to flow, and metabolic effects, such as reduction in the formation of or in the use of high-energy intermediates to drive translocation. An examination of the kinetics of chilling inhibition and recovery in various parts of the plant suggests that the long-lasting inhibition due to sink cooling and the rapid recovery on warming result from the need for continued energy input in the sink region to maintain translocation. In contrast to these characteristics of sink cooling, which indicate inhibition of a process directly involved in moving sucrose, path-cooling characteristics are indicative of physical damage to the system.

The ability of translocation to proceed without impairment through a cooled sugar-beet petiole zone of at least 10-cm length (approximately 50% of the total path) indicates that the mechanism of low-temperature inhibition in the path does not significantly interfere with the energy input required to move the translocation stream. It may be that the energy input required in the path is so low that sufficient energy is available at 0°C or, perhaps more likely, that the degree of damage to the translocation path at 0°C varies between species and is almost negligible in sugar beet. Lowering the temperature below a certain threshold point, characteristic of a given species or ecotype, causes increasing damage to the translocation system. The lack of a major over-shoot upon warming of the low-temperature-acclimated sugar-beet petiole, indicates that recovery at low temperature is the result of a gradual reversal of damage rather than a large increase in the pressure gradient which drives translocation. The lag in recovery upon warming noted for bean (fig. 1) likewise supports the existence of damage which must be repaired before translocation resumes.

CHILLING SENSITIVITY AND RECOVERY

A series of path-chilling experiments by D. E. Bayer (personal communication),

performed on northern and southern ecotypes of Canada thistle (*Cirsium arvense* L.), illustrate a difference in susceptibility to damage within ecotypes of a species. From the data in figure 6, it is apparent that the northern ecotype plant from Montana recovered completely in less than three hours, after 8 cm of stem was held at 0.5°C, while the southern ecotype from California showed no sign of

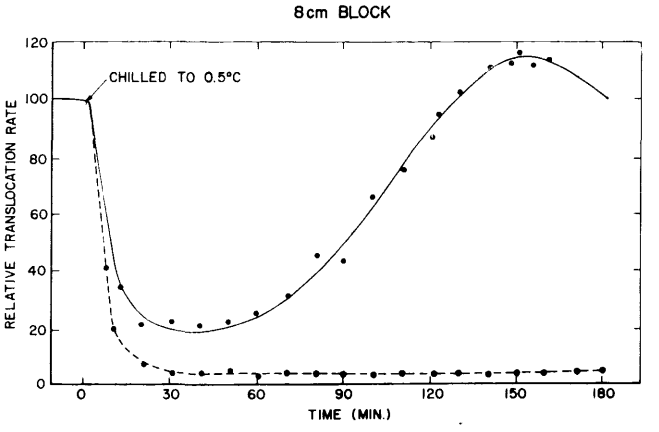

FIGURE 6. Comparison of recovery from path-chilling inhibition in northern and southern ecotypes of Canada thistle. An 8-cm petiole zone was cooled to 0.5°C in each plant. Solid line, northern ecotype; dashed line, southern ecotype. (Bayer, personal communication)

recovery from a similar treatment of 8 cm of stem at 0.5°C over a 3-hr interval. If the stem is not cooled as far below the critical temperature, the effect is lessened (fig. 7) and recovery is considerably more rapid in both ecotypes. The difference in recovery from chilling-induced inhibition of translocation noted previously between bean and beet is seen here in two ecotypes of a single species.

To determine if recovery from chilling inhibition at low temperature is due to a building up of concentration of sugar proximal to the low-temperature zone,

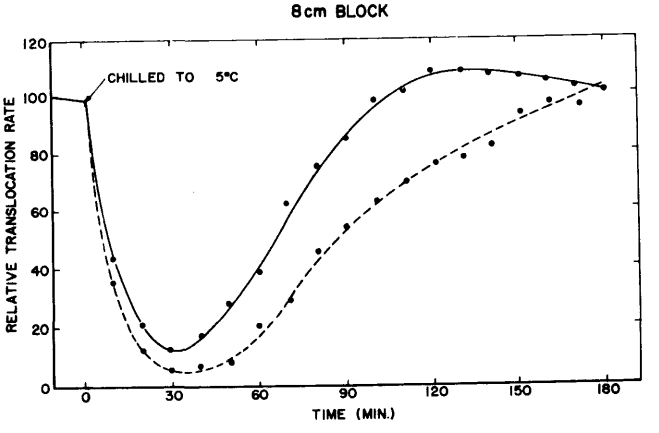

FIGURE 7. Comparison of recovery from path-cooling inhibition at 5°C in northern and southern ecotypes of Canada thistle. An 8-cm zone of petiole was cooled to 5°C. Compare with data from 0.5°C treated plant in FIG. 6. Solid line, northern ecotype; dashed line, southern ecotype. (Bayer, personal communication)

recovery curves for a 2-cm chilled zone of stem (fig. 8) were compared with similar curves from plants with an 8-cm treated zone (fig. 6). Conditions of the experiment were closely controlled to give a high degree of reproducibility for a given treatment. The close agreement of the time course of the two types of experiments indicates that the recovery process is independent of the length of path cooled, and that resumption is not the result of an increased concentration gradient proximal to the temperature block, but rather may be due to a gradual reversal of the effects from cold-induced structural changes.

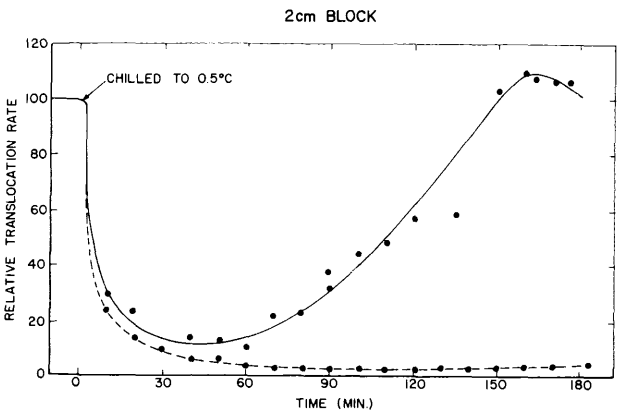

FIGURE 8. Recovery-time course in northern and southern ecotypes of Canada thistle with 2-cm treated petiole zone. Compare these data for a 2-cm zone at 0.5–C with data for 8-cm zone at 0.5°C shown in FIG. 6. Solid line, northern ecotype; dashed line, southern ecotype. (Bayer, personal communication)

POSSIBLE PATH-CHILLING MECHANISMS

Webb (1965) pointed out the similarity of response of cytoplasmic streaming and of translocation to chilling. This correlation alone would not resolve whether cytoplasmic streaming might be responsible for moving the translocate or whether some of the changes that bring about cessation of cytoplasmic streaming might also inhibit movement of the translocate. Cytoplasmic evidence of cold-induced changes in organelles has been observed by Das, Hildebrandt, and Riker (1966) in cells from tobacco, a chilling-sensitive plant. Their time-lapse motion-picture study revealed that cytoplasmic streaming gradually stopped at 5 to -7°C, with a concomitant loss of typical cytoplasmic morphology. During cooling, cytoplasmic strands thinned and numerous small vacuoles formed. The possible relation of these observations to chilling inhibition of translocation remains to be investigated. A correlation between the degree of chilling inhibition and the extent of impedance to flow in the sieve tubes has been theorized by Ford and Peel (1967). These workers have postulated that the inhibition of translocation through a chilled segment of a three- to five-week-old willow shoot is a result of the impedance caused by smaller sieve tubes, whose radii average $12.6 \pm 2.8\ \mu$. When a segment is chilled, other shoots on the same plants, which are two to three years old, show an increase in translocation. Ford and Peel theorized that the difference in response to path chilling in the same plant is a result, in part, of the flow resistance of the larger sieve tubes, which have an average radius of $19.0 \pm 3.9\ \mu$.

Attempts to study sieve-tube structure attest to the lability and fragile nature of the sieve tube, a characteristic which suggests a possible basis of chilling damage. Recent evidence from studies of path-region phloem by Evert, *et al.* (1969), using

improved cytological methods, shows that sieve elements have structural features more characteristic of a typical plant cell than was previously thought to be the case. The presence of highly labile organelles is consistent with the existence of chilling-induced changes in cytoplasmic structure, which could inhibit flow of the translocate. In this manner, chilling would disrupt the translocation path and set a limit on translocate velocity without interfering directly with the energy input responsible for moving the translocate.

The differences in recovery from translocation inhibition for bean versus beet following path cooling resembles the difference in inhibition of cytoplasmic streaming near 0°C observation by Lewis (1956) for chilling-sensitive versus chilling-insensitive plants. In the former category, cytoplasmic streaming ceases or is just perceptible after one to two minutes at 10°C, while in the latter class, streaming proceeds even in the 0-to-2.5°C range for at least several days. A further similarity between inhibition of cytoplasmic streaming and the inhibition of translocation by path cooling is the lag in recovery. Lewis (1956) reported that increased exposure of tomato trichomes to 0°C delayed increasingly the resumption of streaming, while in chilling-insensitive plants, streaming increased markedly in rate within one or two minutes after warming. The lag in resumption of streaming resembles the lag in recovery from chilling-induced translocation inhibition noted by Webb and Gorham for squash (1965), by Thrower (1965) for soybean, and by Swanson and Geiger (1967) for bean.

A basis for the difference in path response between chilling-sensitive and chilling-insensitive plants is suggested by the work of Lyons, Wheaton, and Pratt (1964). A comparison of mitochondria from plants in these two categories revealed a higher unsaturated fatty-acid content and a greater flexibility for membranes from chilling-insensitive plants. These workers suggested that chilling may affect plants by a direct effect on the membranes, or may cause damage to mitochondria and thus disrupt maintenance of cells through inhibition of phosphorylation.

The data from path-chilling experiments suggest that metabolic dependence in the path is limited to the need for energy to maintain structural integrity of the translocation channels, low-temperature inhibition being due to damage to phloem-cell structure concomitant with cooling. Sugar beet, adapted to growth in cold climates, is chilling insensitive and hence blockage of translocation by chilling to 0°C is minimal and transient. It may be that damage to phloem is slight enough in chilling-insensitive plants to permit recovery of translocation without reversal of structural changes. If the decreased translocation is due to a decreased velocity of transport, recovery could be the result of increased sucrose concentration in the sieve sap, which would compensate for the reduced velocity. On the other hand, recovery of chilling-induced structural changes may be more rapid in chilling-insensitive plants. Studies designed to test these hypotheses are in progress.

Bean and other subtropical plants show phloem damage at temperatures considerably above 0°C. In those plants which respond to low temperature in a manner exemplified by bean (e.g., squash, soybean, and tomato), the path-cooling effect may well exert an overriding control of translocation below 5 to 10°C. Highly localized cooling represents an unusual situation for plants under field conditions. Chilling of the entire plant in a chilling-sensitive plant would presumably cause inhibition of translocation mainly by the mechanism of damage. In chilling-insensitive plants, where the damage mechanism is transient and not limiting, mechanisms for fine control of translocation rate and patterns of distribution, in response to supply and demand, would still exert a limit on translocation. These latter mechanisms presumably function in both types of plants, but the damaging effect of low temperature occurs at a considerably higher temperature and the effects are more long-lasting in the chilling-sensitive group.

FUTURE STUDIES

Because the two different temperature responses can be separated in a chilling-insensitive plant, such as sugar beet, it appears that plants of this type are well suited for locating the site at which the translocation process is driven. Localized chilling of the sink region should permit correlation of translocation with respiratory utilization of substrate. These studies, complemented by high-resolution autoradiography, should provide a means of further testing models in which sink unloading is envisioned as helping to motivate translocation (Muller and Leopold, 1966; Esau, Currier, and Cheadle, 1957). Path chilling, coupled with a study of ultrastructure, would help to determine if there is physical damage to the conducting system and to ascertain its nature if found.

It appears that present methodology permits new studies into the nature of low-temperature inhibition in the subdivisions of the translocation system. These studies will help to determine if a given chilling effect is the result of a direct physical change resulting from decreased availability of high energy molecules, or is the result of an effect on a primary metabolic process which drives translocation.

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